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REVISION OF THE WIND RIVER FAUNAS, EARLY EOCENE OF CENTRAL WYOMING. PART 3. MARSUPIALIA

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Abstract

Dental remains of three species of *Peratherium* (*P. comstocki, P. marsupium,* and *P. innominatum*), one species of *Peradectes* (*P. chesteri*) and two species in a new genus, *Armintodelphys* (*A. blacki, A. dawsoni*) are reported from the Wind River Formation, north-central Wyoming. This is the first Wasatchian record of *P. marsupium* and, with *P. innominatum,* the first record of marsupials from the Lysite Member. The range of *P. comstocki* is extended into the early Bridgerian. Review of other Eocene Didelphini indicates that: *Entomacodon minutus* and *Peratherium morrisi* belong in *P. knighti*; *P. innominatum* is a valid species of *Peratherium*; *P. macgrewi* is a subspecies of *P. innominatum*; and *P. knighti* occurs in Wasatchian deposits. Among Peradectini, *Peradectes chesteri* is distinct from *P. protinnominatus* and is morphologically and phylogenetically intermediate in a lineage that includes the latter and *P. minutus* (=*Nanodelphys minutus*); *Armintodelphys* is most closely related to *P. pauli*.

Introduction

Almost one hundred years ago Cope (1884:269) described *Peratherium comstocki* from the "badlands of the Wind River, Wyoming." Since then only three specimens have been added to the marsupial record from the Wind River Formation (Guthrie, 1971), all from the Lost Cabin Member—two were described as *Peratherium* cf. *P. chesteri* and one as *P. comstocki.* Subsequent work by field parties from the Carnegie Museum of Natural History and the University of Colorado

Museum (see Stucky and Krishtalka, 1982) has yielded 47 specimens of didelphids that are referred to three genera and six species. Three are known species of *Peratherium* (*P. comstocki*; *P. marsupium* Troxell, 1923; *P. innominatum* Simpson, 1928), one belongs to *Peradectes (P. chesteri*) and two are new species in a new genus of Peradectini, *Armintodelphys*. Examination of material related to these studies has led to a review of the occurrences, systematics, and evolutionary relationships of Paleocene and Eocene North American didelphids, which will appear elsewhere (Krishtalka and Stucky, 1983*a*).

Abbreviations used in this paper are as follows: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; PM, Field Museum of Natural History; PU, Princeton University (Museum); UCM, University of Colorado Museum; UCMP, University of California Museum of Paleontology; USNM, U.S. National Museum; UW, University of Wyoming; YPM, Yale Peabody Museum; Fm, Formation; loc., locality; L, length; W, width.

LOCALITIES AND AGE

The didelphid material from the Wind River Formation was recovered by surface prospecting and underwater screening of sediments from seven localities in the Lost Cabin Member (CM locs. 34, 1039, 1040, 90, 1085; UCM locs. 79040, 80061), two in the Lysite Member (CM locs. 931, 932), and two in a previously unnamed sequence of strata that is not referrable to either of these members (UCM locs. 80062, 81008; Stucky and Krishtalka, 1982). This sequence is here termed the "Red Creek facies." One of us (Stucky, 1982; in preparation) has proposed that three of the localities in the Lost Cabin Member (CM loc. 34; UCM locs. 79040, 80061) are not Lostcabinian but Gardnerbuttean (Robinson, 1966), which is now thought to represent the earliest part of the Bridgerian, and is older than Bridger A (McGrew and Sullivan, 1970). Briefly, this conclusion is based on: (1) the restriction of *Lambdotherium* to localities in the Red Creek facies and lower part of the Lost Cabin Member of the Wind River Formation, and to localities in other basins in western North America that preserve Wasatchian faunas; (2) the first appearance of *Antiacodon, Trogosus, Palaeosyops, Hyrachyus,* and other taxa at localities in the upper part of the Lost Cabin Member; these localities are stratigraphically above those that record the last appearance of *Lambdotherium*; faunas with these taxa from other basins in western North America have traditionally defined the Bridgerian Land Mammal Age. For the same reasons, an early Bridgerian Age is assigned to faunas from the upper part of the Huerfano Formation (Huerfano B) and the Cathedral Bluffs tongue of the Wasatch Formation, a conclusion also advocated by West (1973), West and Dawson (1973), and Gingerich (1979). The Bridgerian age of taxa from localities in the upper part of the Lost Cabin Member

is reflected in the systematics section below. In addition, we recognize that the Bridger Basin is structurally a part of the Green River Basin. We continue its use as a geographic reference in deference to historical tradition and greater geographic precision.

SYSTEMATICS

Family Didelphidae Gray, 1821

In the most recent review of Tertiary didelphids Crochet (1977, 1979) recognized five genera: *Peratherium* Aymard, 1850 (four species, early Eocene–Oligocene, Europe); *Amphiperatherium* Filhol, 1879 (four species, early Eocene–middle Miocene, Europe); *Herpetotherium* Cope, 1873 (six species, early Eocene–early Miocene, North America); *Peradectes* Matthew and Granger, 1921 (four species, late Paleocene–middle Eocene, North America; two species, early Eocene, Europe); and *Nanodelphys* McGrew, 1937 (two species, middle Eocene–middle Oligocene, North America). Bown and Rose (1979) subsequently named a new didelphid genus, *Mimoperadectes.*

The six species of *Herpetotherium* had long been included in *Peratherium* (Cope, 1884; Simpson, 1928, 1968; Setoguchi, 1975; Green and Martin, 1976), but Crochet (1977) resurrected the former on the basis of two diagnostic features—dominance of stylar cusp D on the upper molars (as opposed to B) and a less reduced talonid on the last molar. These features alone do not seem to warrant recognition of *Herpetotherium,* and are, in any case, variable within and among the North American Eocene species he attributed to *Herpetotherium.* Fox (manuscript; personal communication, 1982), however, recognizes *Herpetotherium* for the type species, *H. fugax,* based on unique features of the anterior dentition, as well as the characters outlined by Crochet (1977, 1979) for the upper and lower molars. Accordingly, *Peratherium* is retained here for five North American Eocene species (see below), at least until *H. fugax*-like anterior dentitions are recovered for these species. In agreement with Bown (1979), and as discussed elsewhere (Krishtalka and Stucky, 1983a), *Nanodelphys* is a junior synonym of *Peradectes.* Thus, recognized genera of North American Tertiary didelphids are: *Peratherium, Herpetotherium, Peradectes, Mimoperadectes,* and a new genus from the Wind River Formation, *Armintodelphys.*

Until most recently, identification of these genera relied primarily on features of the upper molars. Lower molars were thought to be of little diagnostic value until Setoguchi (1973, 1975) and Crochet (1977, 1979) distinguished *Peratherium* from *Peradectes* and *Nanodelphys* on discrete differences in the structure of the hypoconulid-entoconid complex. Bown (1979) and Rose (1981) also adopted these criteria. Cro-

chet's (1979) two tribes of didelphines—Didelphini and Peradectini— can be distinguished by diagnostic characters on their lower molars, including the structure of the hypoconulid, entoconid, and entoconid notch, and the comparative size of the trigonid and talonid. Also useful on the upper molars is the size of the conules, stylar cusp C, and the paracone and metacone, the presence or absence of dilambdodonty, and the shape of the posterolingual area of the protocone.

Tribe Didelphini Crochet, 1979

North American Tertiary genera in this tribe are *Peratherium* and *Herpetotherium*. Unlike members of the Peradectini, these genera have tall, spire-like entoconids, much lower, posteriorly projecting hypoconulids, and deep, wide entoconid notches on M_{1-4}. M^{1-3} have a posterolingually expanded protocone, strong conules and stylar cusp C, dilambdodonty, and lower paracone than metacone.

Peratherium Aymard, 1850

Peratherium (and *Herpetotherium*) are distinct from other genera of North American Tertiary didelphids in three major features of the molar dentition. (1) On M^{1-3} the paracone is at least half the size and height of the metacone—often and in part a function of wear (in unworn specimens the paracone may be only slightly lower than the metacone; see Fig. 4); (2) the centrocrista is dilambdodont; (3) on M_{1-3} the entoconid is large, high and conical, whereas the hypoconulid is a much lower, flat, shelf-like cusp that projects posteriorly behind the entoconid. Although the two cusps are twinned, they are separated by a wide, deep valley (entoconid notch). In the other North American Tertiary didelphids, all of which belong to the Peradectini (except possibly *Thylacodon pusillus*; Krishtalka and Stucky, 1983a), the paracone and metacone are more nearly subequal and not dilambdodont; the entoconid and hypoconulid are smaller, subequal, and more closely twinned; the two cusps arise from a common internal talonid wall and are separated by a much weaker entoconid notch. *Peratherium* lacks the distinctive anterior dentition of *Herpetotherium*.

Our analysis has led to the recognition of five Eocene species of *Peratherium*. In order of decreasing size they are: *P. comstocki* Cope, 1884; *P. edwardi* Gazin, 1952; *P. marsupium* Troxell, 1923; *P. knighti*, McGrew, 1959; and *P. innominatum* Simpson, 1928.

Peratherium morrisi Gazin, 1962, from the Cathedral Bluffs tongue of the Green River Formation, southwestern Wyoming, is a junior synonym of *P. knighti*; the type of the former is indistinguishable from lower molars in McGrew's (1959) hypodigm of *P. knighti*. Setoguchi (1973), misled by Gazin's (1952) figure of *P. morrisi,* erred when he suggested that this species belonged in either *Peradectes* or *Nanodel-*

phys. The type of *P. morrisi* bears the entoconid-hypoconulid structure that is characteristic of *Peratherium* and is close in size to *P. knighti.*

The type of *Entomacodon minutus* Marsh, 1872, is, as suggested by Robinson (1968), a marsupial and is also conspecific with *Peratherium knighti. Peratherium* has priority over *Entomacodon,* as does *E. minutus* over *P. knighti,* but the resultant *P. minutum* (Marsh, 1872) is preoccupied by *P. minutum* (Aymard, 1846). In sum, *P. knighti* includes *E. minutus* and *P. morrisi.* We have identified two teeth (M_1, CM 42139; M_2 or M_3, UCMP 59131) of *P. knighti* from the Four Mile fauna (McKenna, 1960), extending the earliest known record of this species from the early Bridgerian to the early Wasatchian.

Peratherium chesteri Gazin, 1952, from the La Barge fauna, has been transfered to *Peradectes* (Setoguchi, 1973; Bown, 1979), an action with which we agree.

As discussed in detail below, *Peratherium innominatum* Simpson, 1928, belongs in *Peratherium* rather than *Peradectes* (contra Setoguchi, 1973; Bown, 1982), and *P. macgrewi* Bown, 1979 is a Graybullian subspecies of *P. innominatum.*

Finally, although Setoguchi (1973) and Bown and Rose (1979) advocated synonymy of *Peratherium edwardi* Gazin, 1952 with *P. comstocki,* we recommend at least tentative recognition of *P. edwardi.* The type, USNM 19200, and a referred specimen, USNM 19206, both from the La Barge fauna, are, as Gazin indicated, intermediate in size between *P. comstocki* and *P. marsupium*; until a larger sample of this species is recovered, allocation of *P. edwardi* to either *P. comstocki* or *P. marsupium* is unwarranted.

Peratherium comstocki Cope, 1884
(Fig. 1, 2; Table 1, 2)

Type.—AMNH 4252, partial left dentary with M_{2-3}.

Type locality.—Uncertain. Cope (1884) reported the type from the "badlands of the Wind River, Wyoming," and named the species for Professor Theodore D. Comstock, a geologist from Cornell University, who had explored the Wind River region. Matthew (1899:31) listed the type as "*Didelphys*" *comstocki* from the Bighorn Basin, and since then both basins have been cited as the type locality. Matthew (1909: 92), Osborn (1909:46), Troxell (1923) and Hay (1930) favored the Wind River Basin; Simpson (1928) and later students, the Bighorn Basin. Cope (1884) acknowledged his error (Cope, 1880) in describing a Bighorn Basin collection of Eocene vertebrates as coming from the Wind River Basin, but it appears that the three type specimens in that collection did not include AMNH 4252 (Gazin, 1953; Gingerich, 1980). Whatever the answer to this little mystery, *P. comstocki* has since been
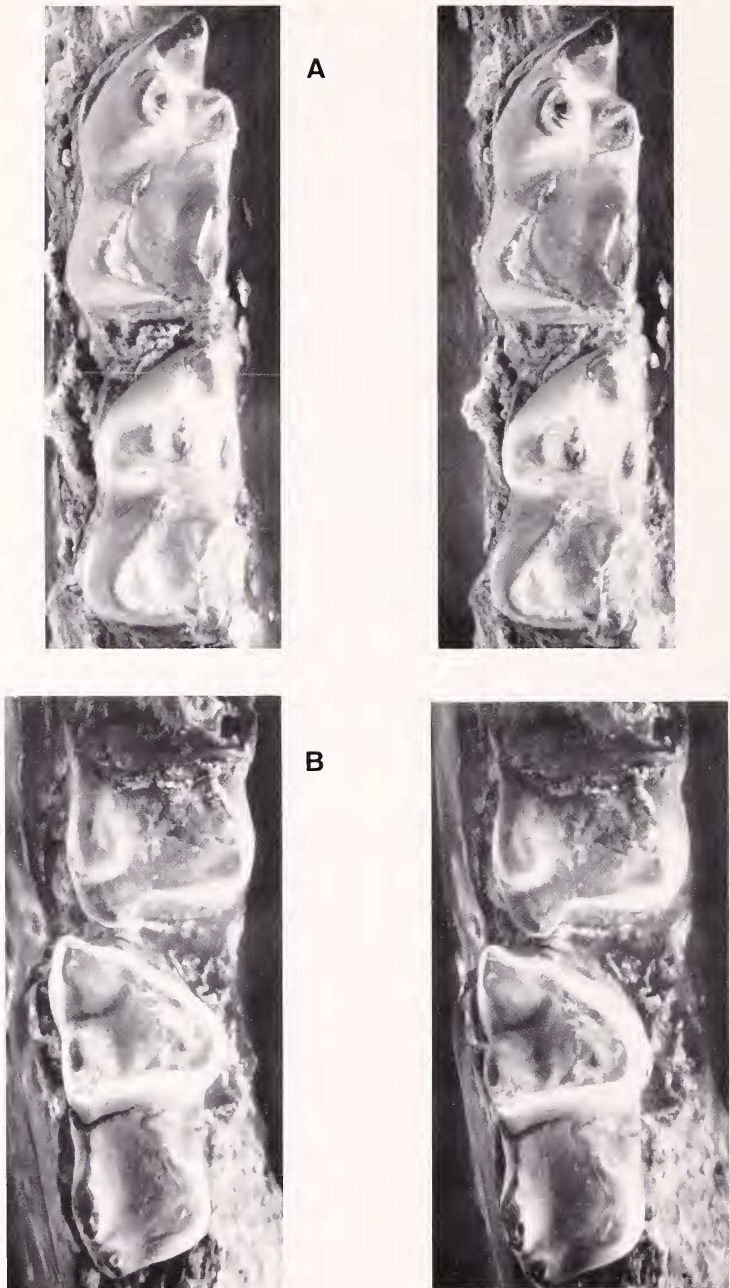
Fig. 1.—*Peratherium comstocki.* (A) CM 55562, LM_{1-2}; (B) CM 21126, LM_{3-4}; both approx. × 15.
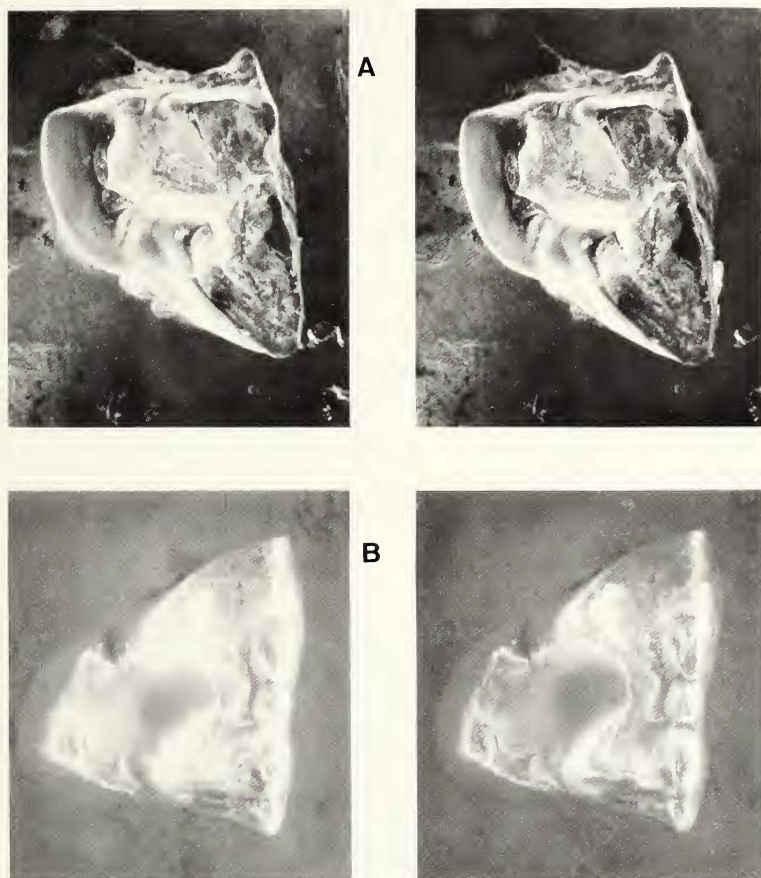
Fig. 2.—*Peratherium comstocki.* (A) CM 35842, LM^1; (B) UCM 44573, RM^2; both approx. $\times$ 14.

recovered from both the Bighorn and Wind River basins (Guthrie, 1971; Schankler, 1980; this paper).

Referred specimens.—M$_{2-3}$—CM 40078, 55567; M$_{1-2}$—CM 55562; M$_{3-4}$—CM 21126; M$_1$—CM 55561; M$_4$—CM 40079; M^1—CM 35842; M^2—UCM 44573; upper molar frag., UCM 45337.

Localities.—CM loc. 34 (Gardnerbuttean, Lost Cabin Member); UCM loc. 80062 (Lostcabinian, Red Creek facies); both in the Wind River Basin (Wind River Fm.), Wyoming.

Known distribution.—Wasatchian—Wind River Basin (Wind River

Table 1.—*Dimensions of lower molars of* Peratherium *and* Armintodelphys, *new genus, from the Wind River Formation, northcentral Wyoming.*

Museum and catalog no.	Locality	M_1		M_2		M_3		M_4	
		L	W	L	W	L	W	L	W
Peratherium comstocki									
CM 55561	34	2.7	1.6						
CM 55562	34	2.7	1.6						
CM 55567	34			3.1	2.0				
CM 55568	34			3.1	2.2				
CM 40078	34			3.0	2.0	3.0	2.0		
CM 21126	34						2.0	3.0	1.4
CM 40079	34							2.9	1.4
Peratherium marsupium									
CM 41157	34		1.3						
UCM 45234	79040			2.7	1.5				
CM 37099	931			2.6	1.6	2.7	1.6		1.2
UCM 42869	79040					2.9	1.7		
Peratherium innominatum									
UCM 44576	80062	1.6	0.8						
UCM 42864	79040	1.8	1.0						
UCM 44866	80061			1.7	1.0				
UCM 42870	79040			1.7	1.0				
UCM 42865	79040			1.9	1.1				
CM 22001	90			1.7	1.0				
CM 36531	34			1.7	1.1				
Armintodelphys blacki									
CM 41159 (Type)	1039					2.2	1.1	2.2	0.9
CM 41161	1040						1.0		
UCM 45252	80061			2.0	1.1				
Armintodelphys dawsoni									
CM 55560	34			1.5	0.9				
CM 55569 (Type)	34				0.8	1.5	0.8		

Fm.), Bighorn Basin (Willwood Fm.), Wyoming; ?San Juan Basin (San Jose Fm., Lucas et al., 1981), New Mexico. Earliest Bridgerian—Wind River Basin (Wind River Fm.), Wyoming; Huerfano Basin, (Huerfano Fm.), Colorado (*P.* cf. *comstocki,* Simpson, 1968). Late Bridgerian— Bridger Basin (Bridger Fm.), Wyoming. Late Bridgerian or early Uintan—Agua Fria (lower Buck Hill Group; West, 1982), Texas.

Emended diagnosis.—Largest known North American Eocene species of *Peratherium*; M^{1-2} with greatly enlarged stylar cusps; labial expansion of stylar cusps B and D create shallow ectoflexus; cusp C medial, equidistant and separate from B and D; lower molars with proportionately longer talonids.

Table 2.—*Dimensions of upper molars of* Peratherium *from the Wind River Formation, north-central Wyoming.*

Museum and catalog no.	Locality	M^1		M^2		M^3		M^4	
		L	W	L	W	L	W	L	W
Peratherium comstocki									
CM 35842	34	3.1	2.8						
UCM 44573	80062			2.8	3.3				
Peratherium marsupium									
CM 41165	1085	2.5	2.6						
UCM 44870	80061					2.7	2.5		
UCM 44580	80062					2.6	2.7		
UCM 44545	79040					2.7	2.9	2.3	2.8
Peratherium innominatum									
UCM 44869	80061	1.6	1.8						
UCM 42872	80061	1.6	1.6						
UCM 45285	80061			1.9	1.7				
UCM 44867	80061							1.3	1.9

Description.—On the first three lower molars the entoconid is large, high and conical, and is isolated from the proximal hypoconulid by a deep, wide notch. The hypoconulid, flat and shelf-like, juts posteriorly behind the entoconid. The talonid is longer and wider than the trigonid, the paraconid is the lowest of the trigonid cusps, and the metaconid is lingual and slightly posterior to the higher protoconid. The precingulid is strong but short, ending posteriorly at the base of the crown below the apex of the protoconid. The hypoconid is broader than the entoconid, but the two cusps are subequal in height. The cristid obliqua is slightly convex labially and meets the trigonid below and labial to the notch of the protocristid. The postcristid descends posterolingually from the apex of the hypoconid to the hypoconulid. From the latter a postcingulid extends labially to the posterior part of the base of the hypoconid.

M_1 is shorter and narrower than M_2 or M_3 and its paraconid leans more anterodorsally. M_4 differs from the other lower molars in having a more elongate talonid that is also narrower than the trigonid, a broader paraconid than metaconid, and in lacking a postcingulid.

The only known M^1 (CM 35842) bears a large metastylar wing and a weak ectoflexus, which is formed by the labial expansion of stylar cusps B and D. The protocone occurs anteriorly, in line with the paracone and stylar cusp B, so that the posterolingual face of the protocone is expanded and slightly "squared-off." The paracone and much higher metacone are subcrescentic and dilambdodont, with a buccally directed centrocrista. The stylar shelf is worn, but it appears that cusp D, elongate in shape, was dominant in the unworn condition, followed in size by cusp B and subequal cusps C and A. A ridge, perhaps developed through wear, joins cusp C to the buccal extension of the centrocrista.

On M^2 (UCM 44573) all of the stylar cusps appear hypertrophied. Cusp D, conical rather than elongate, is slightly larger than cusp B, and both are approximately twice as large as the subequal C and A cusps. Cusp C is equidistant from cusps B and D and directly buccal to the apex of the centrocrista. A slight ectoflexus between cusps B and D is more a function of the labial expansion of these cusps than a true emargination of

the stylar shelf. Cusps B, C, and D are separated by acute notches, whereas a weak ridge connects cusps A and B.

Discussion.—The referred lower and upper molars bear the diagnostic features of *Peratherium* described above. These teeth are significantly larger than those assigned below and in other studies to either *P. marsupium, P. knighti,* or *P. innominatum.* M_2 and M_3 agree in size and structure with those on the type of *P. comstocki.* The first and second upper and lower molars referred here were previously unknown for this species. CM 21126, cited in Guthrie (1971) as M_{2-3}, preserves M_4 and part of M_3.

We agree with Simpson's (1968) allocation of UCM 26541, from the upper part of the Huerfano Formation, to *Peratherium* cf. *comstocki.* This specimen, and those from CM loc. 34 are the first records of this species from the early Bridgerian. CM 13901, M_{3-4} from the upper part of the Bridger Formation, extends the range of *P. comstocki* into the late Bridgerian, and the material from Agua Fria allocated to this species (West, 1982) may be late Bridgerian or early Uintan. Finally, AMNH 56307, originally described as an M_4 of *P. comstocki* from the early Eocene of the Powder River Basin (Delson, 1971), was subsequently identified as an M_2 of *Mimoperadectes* (Bown and Rose, 1979).

Peratherium marsupium (Troxell, 1923)
(Fig. 3; Table 1, 2)

Type.—YPM 13518, partial right dentary with P_3, M_{1-3}.
Type locality.—Bridger Basin, Wyoming.

Referred specimens.—M_{2-4}—CM 37099; M_1—CM 41157, 41158; M_2 or M_3—UCM 42869, 44336, 45234; M_4—UCM 46719; M^{3-4}—UCM 45545; M^1—CM 41165; M^3—UCM 44580, 44870; DP^3—UCM 44574.

Localities.—CM loc. 931 (Lysitean, Lysite Member); CM loc. 34, UCM locs. 80061, 79040 (Gardnerbuttean, Lost Cabin Member); UCM loc. 80062 (Lostcabinian, Red Creek facies); CM loc. 1085 (subage uncertain, Lost Cabin Member); all in the Wind River Basin (Wind River Fm.), Wyoming.

Known distribution.—Wasatchian through Duchesnean—Wind River Basin (Wind River Fm.; Wagon Bed Fm.), Wyoming. Bridgerian—Bridger Basin (Bridger Fm.), Bighorn Basin (Blue Point Member; Eaton, 1982), Wyoming; Uinta Basin (Green River Fm.), Utah (Krishtalka and Stucky, 1983*b*). Late Bridgerian or early Uintan—Sand Wash Basin (Washakie Fm.), Wyoming; Agua Fria (lower Buck Hill Group; West, 1982), Texas.

Emended diagnosis.—Larger than *P. knighti* and *P. innominatum*; smaller than *P. comstocki* and *P. edwardi*; unlike *P. comstocki,* stylar
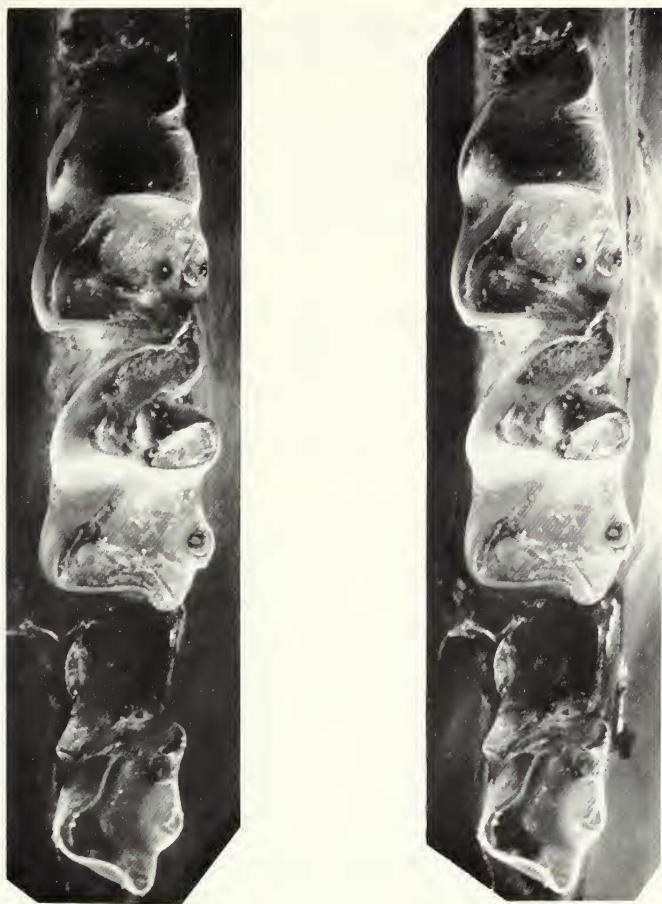
Fig. 3.—*Peratherium marsupium.* CM 37099, LM$_{2-3}$; approx. × 13.

cusps not bulbous labially; unlike *P. knighti,* ectoflexus deeper on M^2 and especially M^3.

Description.—The lower molars closely resemble those of *P. comstocki* except for two features also noted by Simpson (1928): smaller size and slightly shorter talonids in proportion to the trigonids. M^1, like that of *P. comstocki,* has a large metastylar salient, and M$^{1-3}$ have an anterior protocone that is elongated posterolingually. On the only referred M^1—a worn specimen—stylar cusps B and D are subequal and small, followed in size by cusp A and a tiny cusp C. There is no evidence of a cusp E. On M$^{2-3}$ cusp A is absent, cusp C is joined to D, and the metaconule is larger than the paraconule. Unlike on M$^{1-3}$, the paracone is dominant on M^4, cusp A is the only stylar cusp, and the crown

is quadrate. A stylar ridge extends from posterior to cusp A to the area labial to the metacone. The DP³ referred here (UCM 44574) lacks a stylar shelf and has a bulbous metacone.

Discussion. — The recovery of *P. marsupium* from the Wind River Formation represents the first Wasatchian record of this species and, with *P. innominatum,* the first known occurrence of marsupials in the Lysite Member. One of the specimens (CM 23194) that West and Dawson (1975) assigned to *P. marsupium* is closer in size and referred to *P. knighti.*

Peratherium innominatum Simpson, 1928
(Fig. 4; Table 1, 2)

Type. — AMNH 11493, partial left dentary originally preserving M_{1-4}.

Type locality. — Millersville, Lower Bridger, Bridger Basin, Wyoming.

Referred specimens. — M_1 — UCM 44576, 42864, 44606; M_2 or M_3 — CM 22001, 36531, 36967, UCM 44578, 42865, 42870, 42866; M_4 — UCM 44575, 44577; M^1 — UCM 42872, 44869; M^2, M^3 — UCM 46614; M^2 — UCM 45285; M^2 or M^3 — UCM 44868, CM 22000, 55564; M^4 — UCM 44881, 44867, 45255; upper molar fragment, UCM 44579.

Localities. — CM loc. 932 (Lysitean, Lysite Member); UCM locs. 80062, 81008 (Lostcabinian, Red Creek facies); CM loc. 90 (?Lostcabinian, Lost Cabin Member); CM loc. 34, UCM locs. 79040, 80061 (Gardnerbuttean, Lost Cabin Member); all in the Wind River Basin (Wind River Fm.), Wyoming.

Known distribution. — Wasatchian — Wind River Basin (Wind River Fm.), Bighorn Basin (Willwood Fm., record of *P. macgrewi,* see below), Wyoming; Four Mile area (Wasatch Fm.; see below), Colorado. Bridgerian — Wind River Basin (Wind River Fm.), Bridger Basin (Bridger Fm.), Bighorn Basin ("Aycross-like beds," Eaton, 1982), Wyoming; Uinta Basin (Green River Fm.), Utah. Uintan and Duchesnean — Wind River Basin (Wagon Bed Fm.), Wyoming.

Emended diagnosis. — Much smaller than *P. comstocki* and *P. marsupium*; consistently smaller than *P. knighti*; also differs from *P. knighti* in having distinct ectoflexus on M^2 and especially on M^3.

Description. — The lower molars referred here resemble the type, AMNH 11493, in size and in having tall entoconids, low, posteriorly projecting hypoconulids, deep, wide entoconid notches, and compressed trigonids. The upper molars have much higher metacones than paracones and posterolingually expanded protocones. On M^1 (UCM 42872) stylar cusp B is well-developed and equal in size to a twinned C + D cusp, which occurs labial to the premetacrista. The anterior border of cusp C is directly labial to the dorsal apex of the centrocrista and separated by a large gap from cusp B. The stylar shelf is indented by a weak ectoflexus between cusps B and C. Stylar cusp A is extremely weak; there is no cusp E. On M^2 (UCM 45285), B is the largest of the stylar cusps; cusps C and D — proximal but separate — and A are subequal and larger than E.
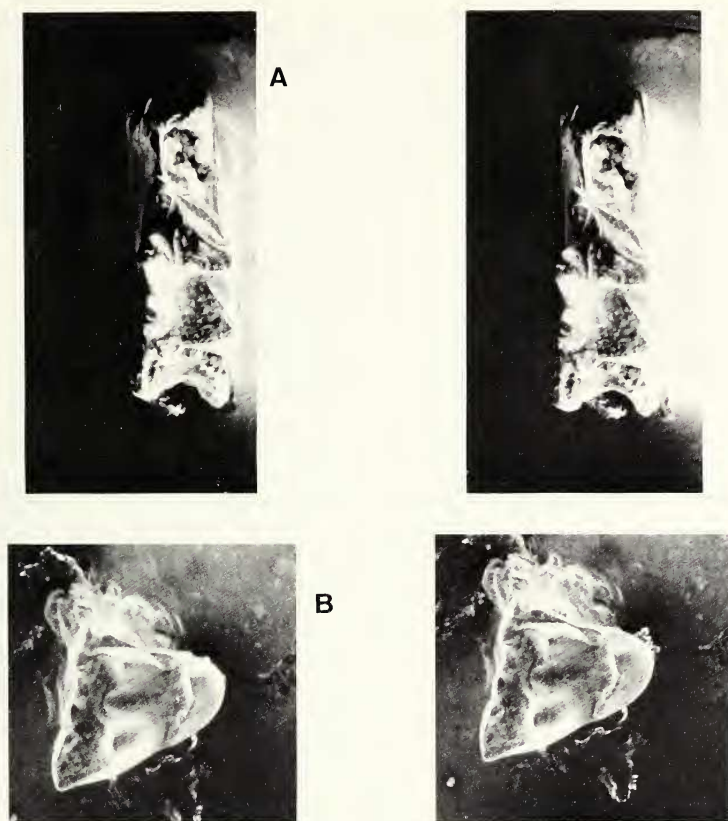
Fig. 4.—*Peratherium innominatum.* (A) CM 36531, RM_2 or M_3, approx. $\times$ 14; (B) UCM 45285, RM^2; approx. $\times$ 11.

Discussion.—Setoguchi (1973) and Bown (1982) allocated *Peratherium innominatum* to *Peradectes.* When Simpson (1928) described the type, AMNH 11493, it preserved M_{1-4}. Unfortunately, M_1 is now missing, and the entoconid and protoconid of M_3 are broken, apparently due to subsequent attempts at further preparation and/or casting of the specimen. Nevertheless, the size of the entoconid on M_2 and its broken base on M_3 is clearly *Peratherium*-like. In these diagnostic features, as well as in the size and morphology of M_{2-4}, AMNH 11493 is virtually identical to large samples of *Peratherium* from Powder Wash, Uinta Basin, and from the Wind River Formation. These samples are described here and elsewhere (Krishtalka and Stucky, 1983*b*) as *Peratherium innominatum.*

The two teeth (CM 22000, CM 22001) that Guthrie (1971) assigned to *Peratherium* cf. *P. chesteri* are referred here to *P. innominatum*. A lower jaw that West (1973, Pl. 1, Fig. B; PM 15320) figured and referred to *P. innominatum* may not be a marsupial; two other specimens (West, 1973: Pl. 1, Fig. C, D; PM 15682, PM 15866) he identified as *P. innominatum* are referrable to *Peradectes chesteri*. UW 984 from Tabernacle Butte, identified as *Peratherium* cf. *innominatum* by McGrew (1959), bears the diagnostic features of *Peradectes* and is referred below and elsewhere (Krishtalka and Stucky, 1983a) to *P. chesteri*. Our analysis of the Badwater late Eocene didelphids indicates that Setoguchi's (1975) sample of *Peratherium* cf. *P. knighti* includes specimens of *P. knighti* and *P. innominatum*.

P. innominatum is closest in size and morphology to *P. knighti* and *P. macgrewi*. The teeth are smaller than those of *P. knighti* and M^{2-3} have more distinct ectoflexi. Distinction of *P. innominatum* from *P. macgrewi* other than on mean size is not possible with the known material. Except for M_1, upper and lower molars of *P. innominatum* are slightly but consistently larger. The current stratigraphic record and the close similarity between the Graybullian *P. macgrewi* and the Lysitean through early Bridgerian *P. innominatum,* imply an ancestor-descendant relationship between the two that involved a slight increase in size. Similar anagenetic increase in size occurs between the Wind River Formation population of *P. innominatum* and that from Powder Wash, Green River Formation, Utah (Krishtalka and Stucky, 1983b). *P. macgrewi* is reduced in rank to a subspecies of *P. innominatum* for biostratigraphic purposes (Simpson, 1961:175).

Peratherium innominatum macgrewi (Bown, 1979), new rank

This temporal subspecies of *P. innominatum* is known only from Graybullian horizons in the Bighorn Basin and the Sand Wash Basin. We have identified an isolated M_2 or M_3 (CM 42137) of *P. i. macgrewi* from Sand Quarry, Four Mile fauna, Colorado. Also, as noted by McKenna (1960, Fig. 18a), UCMP 44095 from Kent Quarry is *Peratherium*-like. The disparity in height between the paracone and metacone on M^{1-2}, the dilambdodont centrocrista, and the expanded posterolingual area of the protocone distinguish this specimen from contemporaneous *Peradectes* in the Four Mile sample. The size of M^{1-2} on UCMP 44095 is within the range of these teeth in the hypodigm of *P. i. macgrewi* from the type area (Bown, 1979). Also, one of the upper molars in UW 9742 that Bown (1979, Fig. 40A, center) identified as *P. chesteri* is dilambdodont and belongs to *P. i. macgrewi*.

Tribe Peradectini Crochet, 1979

North American Tertiary genera in this tribe are *Peradectes* (including *Nanodelphys,* see Bown, 1979; Krishtalka and Stucky, 1983a),

Mimoperadectes, and *Armintodelphys,* the new genus from the Wind River Formation. They differ from *Peratherium* in that M_{1-4} bear a low or very reduced entoconid, a closely twinned and dorsally projecting hypoconulid, and a weak or vestigial entoconid notch. Additionally, M^{1-3} have a V-shaped protocone (no posterolingual expansion), conules and stylar cusp C that are small to absent, no dilambdodonty, and a paracone that is as high as or slightly lower than the metacone.

Peradectes Matthew and Granger, 1921

Peradectes is much smaller than *Mimoperadectes* and has a larger metaconid than paraconid on M_{2-4}. Compared to *Armintodelphys,* lower molars of *Peradectes* retain subequal hypoconulid and entoconid and an entoconid notch.

Our revision of the systematics of Paleogene North American didelphids (Krishtalka and Stucky, 1983*a*) indicates that there are six discernable species of *Peradectes*: *P. elegans* Matthew and Granger, 1921; *P. pauli* Gazin, 1956; *P. protinnominatus* McKenna, 1960; *P. chesteri* (Gazin, 1952); *P. californicus* (Stock, 1936; see Lillegraven, 1976); *P. minutus* (McGrew, 1937). Of these, only *P. chesteri* has been found in the Wind River Formation. *Thylacodon pusillus* may also be a species of *Peradectes* (Clemens, 1979) and is under study elsewhere (see Archibald, 1982).

Peradectes chesteri (Gazin, 1952)

Type.—USNM 19199, right partial dentary with M_3.

Type locality.—Upper part of the Wasatch Formation (="Upper Knight beds"), La Barge, Wyoming.

Referred specimen.—M^1—UCM 45288.

Locality.—UCM loc. 80061 (Gardnerbuttean, Lost Cabin Member), Wind River Basin (Wind River Fm.), Wyoming.

Known distribution.—Late Wasatchian—Green River Basin (Wasatch Fm.), Wyoming. Bridgerian—Wind River Basin (Wind River Fm.), Green River Basin (Bridger Fm.), Wyoming; Uinta Basin (Green River Fm.), Utah.

Emended diagnosis.—Compared to *P. elegans*: teeth smaller; M_1 smaller than M_2; M_3 talonid narrower (basally) than trigonid; compared to *P. elegans* and *P. pauli*: P_3 lower than M_1 and with shorter talonid; M_4 talonid shorter than trigonid; compared to *P. elegans, P. pauli* and *P. protinnominatus*: M_{1-3} talonids with narrower occlusal width (hypoconid more internal); compared to *P. elegans, P. pauli, P. protinnominatus* and *P. californicus*: greater disparity in L/W ratio from M^1 to M^3; conules and stylar cusps vestigial; M^3 more transverse with a more highly compressed protocone; M_{1-3} narrower in proportion to

length, with no labial emargination between trigonid and talonid; compared to *P. californicus*: P_3 talonid present; compared to *P. minutus*: M^{1-3} paracone higher than protocone and stylar cusp B; stylar cusp B not enlarged; M^3 and especially M^2 less transverse, with less compressed protocone; gap between M_4 and ascending ramus present.

Description. — The isolated M^1 (L = 1.2; W = 1.1) is abraded, but preserves the diagnostic features of the species. As in the sample of upper molars from Powder Wash (Krishtalka and Stucky, 1983*b*), the paracone is slightly lower than the metacone, but higher than the protocone and stylar cusp B. Conules and stylar cusps other than B are absent or were worn away.

Discussion. — Setoguchi (1973) and Bown (1979) correctly allocated *Peratherium chesteri* to *Peradectes,* based on the entoconid-hypoconulid configuration on the lower molars. These authors and Rose (1981) also considered *P. chesteri* a senior synomym of *P. protinnominatus,* a conclusion that is at odds with our analysis of the material. As discussed elsewhere (Krishtalka and Stucky, 1983*a*), *P. protinnominatus* is a valid species and includes the Clarkforkian and early Wasatchian material from the Bighorn Basin that Bown (1979) and Rose (1981) referred to *P. chesteri*.

The most complete known specimen of *P. chesteri* is UW 984, a lower jaw with P_3–M_4 from Tabernacle Butte, which was previously identified as *Peratherium* cf. *innominatum* (McGrew, 1959) and *Peradectes* sp. cf. *P. innominatus* (Bown, 1982). *P. innominatum* was shown above to be a species of *Peratherium* rather than *Peradectes,* and UW 984 bears the hypoconulid-entoconid complex of the latter. M_3 on UW 984, as on the type of *P. chesteri,* is smaller than that of *P. elegans* and has a narrower talonid than trigonid. It is also smaller than M_3 of *P. pauli* and *P. protinnominatus,* and the buccal contour at the base of the crown between the trigonid and talonid is less emarginate. In addition, the morphology of P_3–M_4 on UW 984 indicates that, in contrast to *P. elegans, P. pauli* and *P. protinnominatus*: molars of *P. chesteri* have lower trigonids; P_3 is lower than M_1, M_{1-3} are narrower in proportion to length, have narrower talonids and a more nearly straight buccal margin basally; and M_4 has a shorter talonid than trigonid. Unlike the condition in *P. elegans,* M_1 is smaller than M_2. *P. chesteri* differs from *P. californicus* in having a talonid on P_3 and from *P. minutus* in retaining the gap between M_4 and the ascending ramus.

Apart from the single upper molar referred here, upper molars of *P. chesteri* have been recovered from Powder Wash (Krishtalka and Stucky, 1983*b*) and the Green River Basin (West, 1973, Figs. C, D; PM 15682, PM 15866). They differ from upper molars of all North American species of *Peradectes* except *P. minutus* in having more transverse M^{2-3}, vestigial conules and stylar cusps C and D, and a more com-

pressed protocone, especially on M^3. In contrast to *P. minutus,* in *P. chesteri* M^{1-3} have a higher paracone than protocone and stylar cusp B, and a smaller stylar cusp B, and M^2 is less transverse, with a less compressed protocone.

The features of the upper and lower dentition of *P. chesteri,* and its temporal distribution, suggest that this species is intermediate morphologically and phylogenetically between *P. protinnominatus* and *P. minutus.*

Armintodelphys, new genus

Etymology.—Arminto, a hamlet in Natrona County, Wyoming; *delphys,* Gr., womb, a common suffix for generic names of marsupials.

Type species.—*Armintodelphys blacki,* new species.

Included species.—Type species and *A. dawsoni,* new species.

Diagnosis.—Differs from all North American Tertiary didelphines as follows: 1) entoconid lower and smaller than the hypoconulid, with no entoconid notch; 2) talonid narrower (basally) than the trigonid on M_{1-2}. Smaller than *Mimoperadectes* and with smaller paraconid than metaconid on M_{2-4}.

Known distribution.—Latest Wasatchian to earliest Bridgerian—Wind River Basin (Wind River Fm.), Wyoming.

Discussion.—*Armintodelphys* is the fifth known genus of North American Tertiary didelphines and, along with *Peradectes* and *Mimoperadectes,* is included in the Tribe Peradectini Crochet, 1979 (as emended here).

Armintodelphys is more derived than species of *Peradectes* in having an entoconid that is much smaller and lower than the hypoconulid on M_{2-4}. *Peradectes* retains the primitive condition (for the Peradectini) of an entoconid that is slightly taller than or subequal to the hypoconulid. A revision of the species of *Peradectes* (Krishtalka and Stucky, 1983*a*) indicates that *Armintodelphys* most closely resembles *Peradectes pauli* in the buccal emargination of the base of the crown between the trigonid and talonid of M_{2-3}, the longer talonid than trigonid on M_4, and the narrower talonid than trigonid on M_3. These features imply that *Armintodelphys* evolved from or shared a common ancestry with *P. pauli.*

Armintodelphys blacki, new species
(Fig. 5; Table 1)

Etymology.—Named in honor of Craig C. Black for his contribution to the paleontology of the Wind River Basin.

Type.—CM 41159, partial left dentary with M_{3-4} and alveoli for P_3–M_2.

Type locality.—CM loc. 1039 (Buck Spring: Lost Cabin K-5), Lost Cabin Member, Wind River Formation, Natrona County, Wyoming.

Referred specimens.—Dentary fragment with M_3 talonid—CM 41161; associated P_3, M_1 trigonid, M_2, M_3 trigonid—UCM 45252.

Localities.—Type locality (Lostcabinian, Lost Cabin Member) and UCM loc. 80061 (Gardnerbuttean, Lost Cabin Member), both in the Wind River Basin (Wind River Fm.), Wyoming.

Known distribution.—Late Wasatchian to earliest Bridgerian—Wind River Basin (Wind River Fm.), Wyoming.

Diagnosis.—Largest species of *Armintodelphys*; no posterior cingulid on M_{2-3}.

Description.—Upper molars of *A. blacki* have not been recovered. The dentary, long and slender as in other didelphines, is 4.5 mm deep below M_4. The inflected angle begins just below the coronoid process and the mental foramen occurs directly below the posterior root of P_3. Alveoli preserved on the type specimen indicate that there were no diastemata between the anterior premolars. P_3 is premolariform. The single, dominant cusp—the protoconid—bears a posterolabial crest that extends from its apex to the labial border of the postcingulid, as in *Peradectes* and *Peratherium,* but in contrast to *Mimoperadectes* where this crest is posteromedial (Bown and Rose, 1979, Pl. 1, Fig. 2). No talonid cusps are present, but a talonid basin is developed posterolingual to the protoconid and anterior to the strong postcingulid.

The cusps on the trigonid fragment of M_1 are similar in size and position to M_1 of *Peratherium* and *Peradectes.* The paraconid is anterior and almost as high as the metaconid, which is directly lingual to and lower than the protoconid. Compared to M_1, the trigonids on M_2 and M_3 are wider and more compressed anteroposteriorly. A groove on the anterior face of the paraconid receives the hypoconulid of the anterior molar. On M_{2-4} the talonid is narrower than the trigonid and the cristid obliqua meets the posterior wall of the trigonid labial to the protocristid notch. The buccal base of the crown is excavated between the talonid and trigonid. A wear facet in the hypoflexid notch descends the posterior face of the trigonid to the dento-enamel border of the tooth, suggesting that, as in *A. dawsoni,* the paracone on the upper molars was as tall as the metacone. The entoconid, smaller than in *Peratherium, Peradectes,* and *Mimoperadectes,* and well-removed from the metacone, occurs on a lingual ridge that runs from the metaconid to the hypoconulid. The latter is the tallest talonid cusp and lies posterolabial to the entoconid. On M_{2-3} the talonid notch is lower than the point at which the cristid obliqua meets the trigonid. M_4, known only in the type, resembles M_{2-3} but has a more elongate talonid, with a more medial and posteriorly projecting hypoconulid.

Armintodelphys dawsoni, new species
(Fig. 5; Table 1)

Etymology.—Named in honor of Mary R. Dawson for her contributions to the paleontology of the Wind River Basin.

Type.—CM 55569, partial dentary with talonid of M_2, M_3, and trigonid of M_4.

Type locality.—CM loc. 34 (Davis Ranch, also called Sullivan Ranch; "maroon shale" layer of Guthrie, 1971), Lost Cabin Member, Wind River Formation, Wind River Basin, Natrona County, Wyoming.

Fig. 5.—*Armintodelphys,* new genus. (A) *A. dawsoni,* new species, CM 55569, RM_{2-4} (type); (B) *A. blacki,* new species, CM 41159, LM_{3-4} (type); both approx. $\times$ 15.

Referred specimen.—M_2—CM 55560.

Localities.—Type locality (Gardnerbuttean) only.

Known distribution.—Early Bridgerian—Wind River Basin (Wind River Fm.), Wyoming; Uinta Basin (Green River Fm.), Utah.

Diagnosis.—Smallest species of *Armintodelphys*; differs from *A. blacki* in having a postcingulid on M_{2-3}.

Description.—The depth of the mandible below M_4 is 2.7 mm in the type specimen. Apart from the differences cited in the diagnosis, the lower molars compare favorably to those of *A. blacki* described above.

OCCURRENCES AND RELATIONSHIPS

Three lineages of *Peratherium*—*P. comstocki, P. knighti,* and *P. innominatum*—differing mainly in size, appear abruptly in the early Wasatchian; *P. comstocki* extends to the early Bridgerian, and the other two into the Duchesnean. A fourth, *P. marsupium,* ranges from the middle Wasatchian to the Duchesnean, and a fifth, *P. edwardi,* is known only from the late Wasatchian. Anagenetic change in these species is small or undetectable; four of the species are stable, whereas *P. innominatum* appears to undergo a slight increase in size. Three of these species (*P. innominatum, P. marsupium, P. comstocki*) are present in the Wind River Formation. They occur in lithosympatry at only two of the eleven localities that yielded marsupial material (CM loc. 34; UCM loc. 80062).

The Peradectini are represented in the Wind River Formation by two species in a new genus, *Armintodelphys* (*A. blacki* and *A. dawsoni*), and by *Peradectes chesteri. Armintodelphys* is most closely related to *Peradectes pauli. P. chesteri,* known from late Wasatchian to late Bridgerian horizons, appears to be morphologically and phylogenetically intermediate between *P. protinnominatus* and *P. minutus.* If this inference is correct, trends in the *P. protinnominatus-P. chesteri-P. minutus* lineage involved the development of more transverse M^{2-3} with a more compressed protocone, and reduction in the crown height of the upper and lower molars, in the conules and stylar cusps C and D, in the length and width of the talonid on the lower molars and in the buccal emargination between the talonid and trigonid on M_{1-3}.

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